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REGENERATION PATTERN OF *POA FOLIOSA* HOOK F. ON MACQUARIE ISLAND

By D. H. Ashton

Botany Department, University of Melbourne

Abstract

Poa foliosa is a tussock-forming perennial which develops a high pedestal or stool of fibrous peat under its crown. Its rhizomes grow sympodially by means of long and short shoots. The tussock may consist of more than one genotype, since it may initially develop from the random juxtaposition of several different rhizomes. Once a high pedestal of peat is formed the rhizome system is confined to it. The pattern of regeneration of *Poa foliosa* suggests Cyclic Development throughout Pioneer, Building, Mature, Degenerate phases, and a Gap stage which involves small herbs, grasses, and bryophytes, or the large herbaceous *Stilbocarpa*. Regeneration of *Poa foliosa* is almost exclusively by means of rhizomes. The growth rate of *Poa foliosa* is high in spite of the uniformly cool climate, and as much as one-third of the weight of the tops is replaced in the first year following defoliation.

Introduction

The Australian National Antarctic Research Expedition (ANARE) has maintained a scientific station at Macquarie Is. since 1948. Taylor (1955) has fully described the major plant associations occurring in the five vegetation formations of Grassland, Herbfield, Feldmark, Fen, and Bog, and has assessed their controlling environmental factors. In December of 1962, 1963, and 1964, the author visited Macquarie Is. with the ANARE for 6-7 days to make further investigations of the grassland.

The object of the present short-term study has been to investigate the way in which the grassland perpetuates itself and maintains a luxurious cover in an environment which causes winter dormancy in most temperate plants.

General Environment

Macquarie Is. lies at 54°S. and 159°E., isolated midway between Tasmania, New Zealand, and the Antarctic continent. It is a narrow plateau 21 miles long and 2-3 miles wide, with slopes of 20-40° which rise to altitudes of 900-1,423 ft. Its long axis runs almost N.-S., astride the full force of the westerly storms. The N. third of the island consists of a pre-Tertiary series of basalts and intrusive gabbros and peridotites, and the remaining two-thirds consists of a mid-Tertiary series of submarine basalts (Law & Burstall 1956). The island is the remains of a block fault elevated from considerable depths. The extensive glaciation in the Pleistocene period has resulted in a smoothed topography with a mantle of glacial till, cirques, and many lakes and tarns. A wide shore platform occurs above sea level around much of the island but is interrupted by screes, sand, and shingle beaches and by blown grey sand on the W. side.

The majority of soils below 800-900 ft are known as Highmoor Peats (Taylor 1955) and support Tussock grassland and some Herbfields. Commonly 1-3 ft of peat is developed over old screes or rocky yellow to brown clays. Phosphorus analyses given by Taylor indicate that the fertility of the peat is likely to be considerably lower than the subsoils, the lower layers of peat being particularly poor. The pH varies from 4·2-4·5 in the peat to 6·0 in the subsoil. Some Herbfield soils on E. slopes at 600-700 ft have 6-12 in. of brown friable loam grading into

2-3 ft of yellow clay to clay loam and, in this respect, are similar to the Alpine Humus soils of SE. Australia. The clay subsoils in many soils are mottled red and light grey, indicating conditions of severe waterlogging. In areas of low relief such as shore platforms and shallow valleys, drainage is impeded, and fibrous or amorphous peat may accumulate to depths of up to 14-16 ft, and have a water-table within 12 in. of the surface (Fen and Bog peats, Taylor 1955). On the wind-exposed slopes of the plateau above 700-800 ft, terracing occurs in association with feldmark vegetation. The gravelly loams in these localities are frequently strongly patterned by frost sorting (Tilley 1964). A high water-table occurs in these soils in the vicinity of lakes and tarns.

The climate of Macquarie Is. is almost uniformly cloudy, windy, wet, and cold. Precipitation occurs on about 330 days per year, culminating in only 40 in. per year at sea level. Snow may fall in any month but is light and does not persist long even in winter. Sunshine averages 2·2 hours per day (3 hours per day in summer, ½ hour per day in winter), 18% of that possible at 54°S. latitude (Law & Burstall 1956). The median wind speed is 20 knots, there are few calms and occasionally gales of over 80 knots are experienced. Two-thirds of all winds blow NNW. to WSW. The relative humidity is always high, averaging 88%, and salt spray blowing or drifting onshore as a light mist is an important feature of the environment. The mean monthly air temperatures at the ANARE station show a remarkably small variation from 37·1°F in June to 43·8°F in January, although the temperature extremes range from 17°F grass temperature to 53°F air temperature. The mean diurnal range is only slightly less than the mean seasonal range.

Vegetation and Location of Sites of Study

Macquarie Is. is devoid of trees and shrubs and, at lower altitudes (less than 600 ft elevation), a dense tussock grassland of *Poa foliosa* clothes the slopes and flats in all sites where the water table is more than one foot from the surface (Fig. 1). It is not continuous but is scarred by old and young screes and landslips in various stages of plant succession (Pl. 27, fig. 1, 2). These grasslands have an exact counterpart on other southern oceanic islands and have been termed Maritime Tussock formation by Warming (1909), Maritime Tussock Moor by Cockayne (1928), and Maritime Tussock grassland by Wace (1960).

The grassland is composed of massive tussocks up to 4-5 ft high and 2-5 ft in diameter, with the crowns interlacing or spaced up to one or rarely two diameters apart (Pl. 27, fig. 3). The growth is so dense and rank that associated species are confined to the gaps between the tussocks. *Stilbocarpa polaris* is the commonest associate occupying the same structural stratum as *Poa foliosa* and, in sites with W. exposures or in the early stages of landslip or rock scree succession, it may co-dominate. On sheltered E. aspects the large tufted fern *Polystichum vestitum* may become locally common.

From 600-900 ft in sheltered sites and, on areas with high water-tables, the tussock grassland gives way to the floristically richer herbfields. These are characterized by the large rosette composite *Pleurophyllum hookeri* which is associated with *Stilbocarpa* and the stoloniferous grasses *Festuca erecta* and *Agrostis magellanica*. Numerous other herbs, sedges, and bryophytes are present and, at higher elevations, cushions of *Azorella selago* herald the change to the Feldmark communities. On the steep slopes, areas of grassland and the accumulation of peat may slump and shear off, exposing mineral soil and rock scree. Here, in the absence of *Poa foliosa*, most members of the herbfields become established during the process of succession (Taylor 1955). Ultimately, however, *Poa foliosa* re-

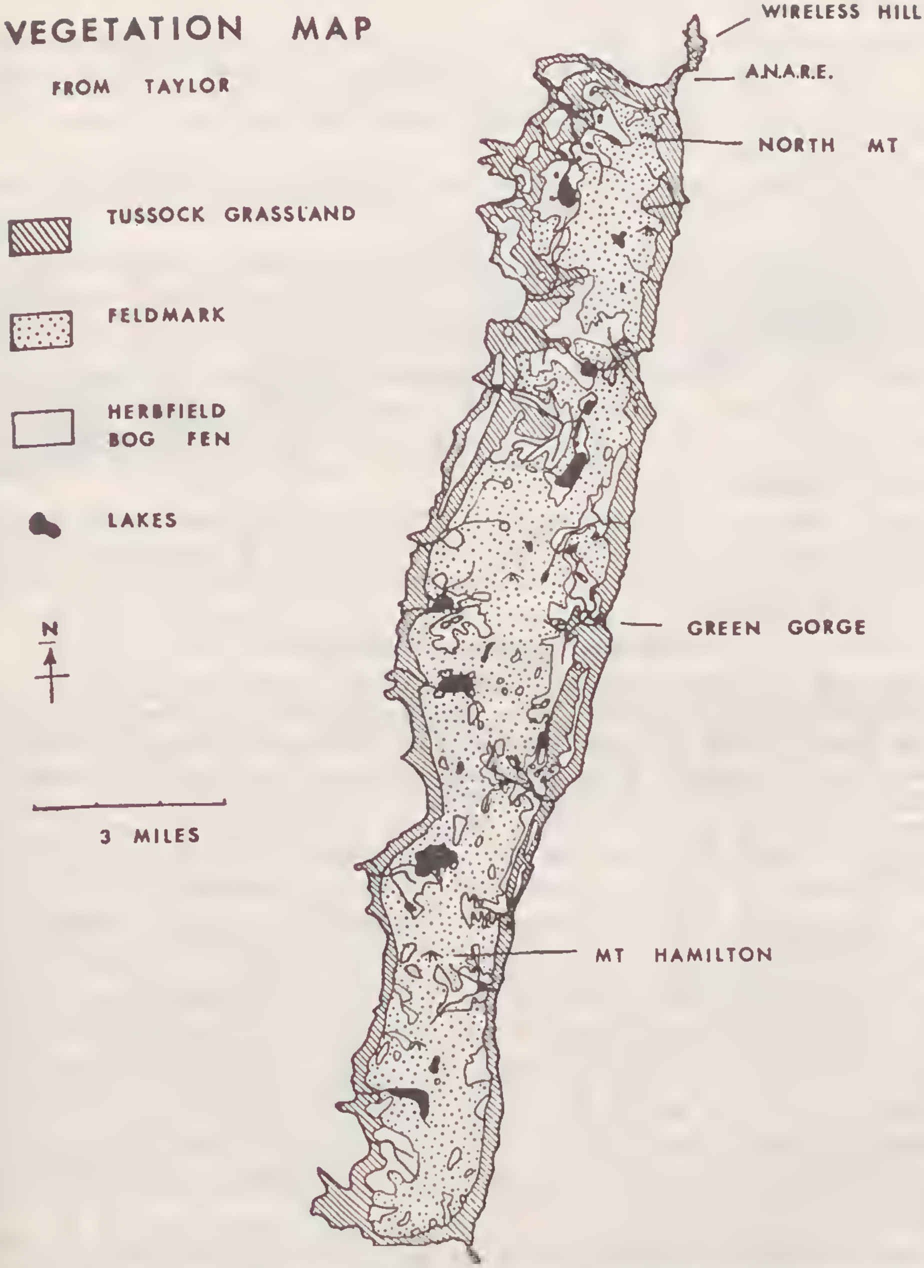


FIG. 1—Map of Macquarie Is. showing distribution of major vegetation formations, from Taylor (1955).

establishes its cover and dominance and the herbfield species are eliminated or reduced to insignificant proportions.

Penguin rookeries and elephant seal wallows have disturbed the grassland areas in the coastal fringe (Gillham 1961) and rabbits have spread widely over the S. three-quarters of the island, causing considerable damage (Costin & Moore 1960). Sheep also caused damage on Wireless Hill during the last decade, but these have now been destroyed.

The three sites chosen for study are out of the range of disturbance by biotic factors and are situated within half a mile of the ANARE station at the N. end of the island.

SITE 1: This is at the SE. corner of Hasselborough Bay on an old scree delta 50 ft above sea level, with a slope of 10-15° to the N. This community corresponds to the *Poa foliosa-Stilbocarpa polaris* association of Taylor. The *Stilbocarpa* makes up 10-15% of the total cover.

SITE 2: This is on the N. side of Buckles Bay at the base of Wireless Hill, 20 ft above sea level on the clay-rock rubble of a very old peat landslip. It has a slope of 25-30° to the S. and is protected by a small hill (Camp Hill) adjacent to the ANARE station. This corresponds to the *Poa foliosa-Cardamine corymbosa* association of Taylor.

SITE 3: This is on a westerly slope of 5-6° on a flattened shoulder of Wireless Hill 250 ft above Hasselborough Bay. This association is similar to, but less luxuriant than Site 2, and presents clear evidence of succession from an old peat slip to tussock grassland.

Growth Habit of *Poa foliosa*

The trunk or pedestal of fibrous peat supporting the large litter-girded crown was the outstanding characteristic of this grass noted by the early plant geographers.

The fibrous peat of the pedestal consists of an extremely dense mass of living and dead roots, a network of living and dead rhizomes, and the dead remains of the enveloped leaf bases and culms. There is a reasonably distinct boundary between the pedestal and the dark amorphous peat of the top 1-3 ft of the soil.

On flat or gently sloping ground the pedestals may be 6-22 in. high. On steep slopes, however, the tussocks are unstable and become prostrate on the ground or on other tussocks below. Although the tussocks have powers of regeneration for a considerable length of time, they may nevertheless die out, leaving the pedestal mounds in various stages of humification (Fig. 2, 3).

Poa foliosa develops and spreads almost entirely by its complex rhizome system. Proven seedlings are distinctly rare and most small plants excised from the peat show evidence of an original rhizomic connection. The rhizome is essentially sympodial, consisting of long and short shoots. The long shoot is ultimately terminated by a short shoot but, more commonly, the latter develops from an axillary bud of either shoot type. The short shoot may be sessile or connected to the parent rhizome by one or two internodes. The distinction between the two shoot types is therefore somewhat arbitrary.

The long shoots extend for 2-8 in. and have hollow internodes ½-2 in. long. They bear scale leaves and roots at the nodes but, in vigorously advancing margins, rudimentary or normal leaves may develop. The vegetative short shoots may be ½-2 in. long and bear 5-30 congested nodes. In December, the first-formed bracts and rudimentary leaves at the base of the shoot are dead. Three to four tough V-shaped mature leaves are developed which have laminas 24-30 in. long and pallid sheaths 4-9 in. long. Three immature folded leaves enclose the apical bud.

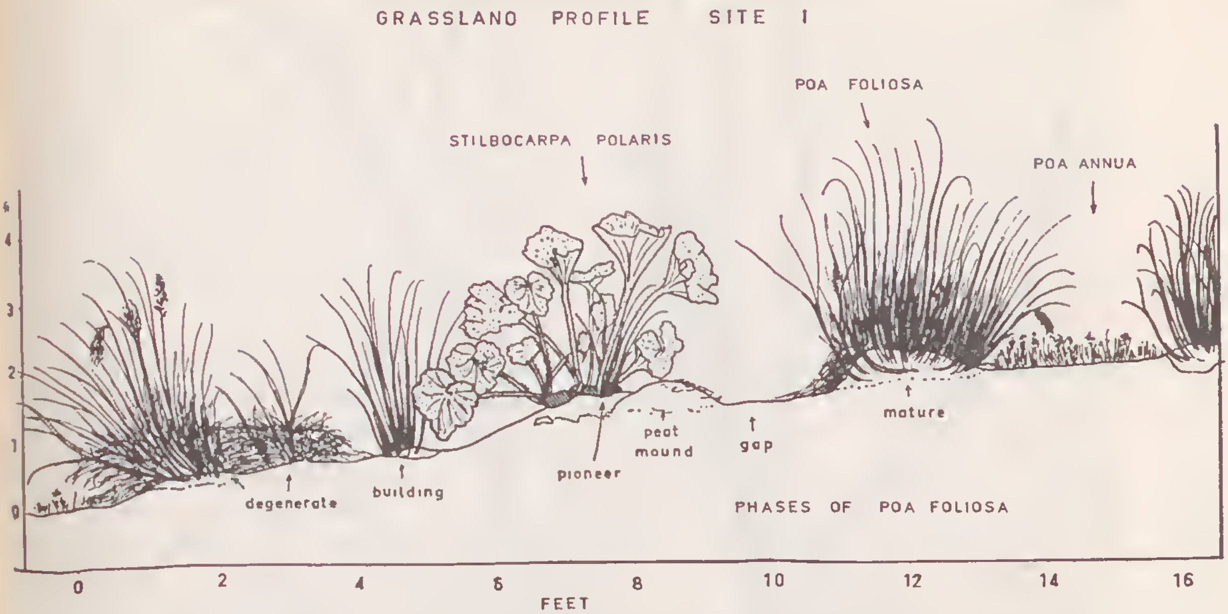


Fig. 2—Profile of *Poa foliosa-Stilbocarpa polaris* tussock grassland at site 1, showing phases of *Poa foliosa*, old peat mounds, and the invasion of *Stilbocarpa* by *Poa foliosa*.

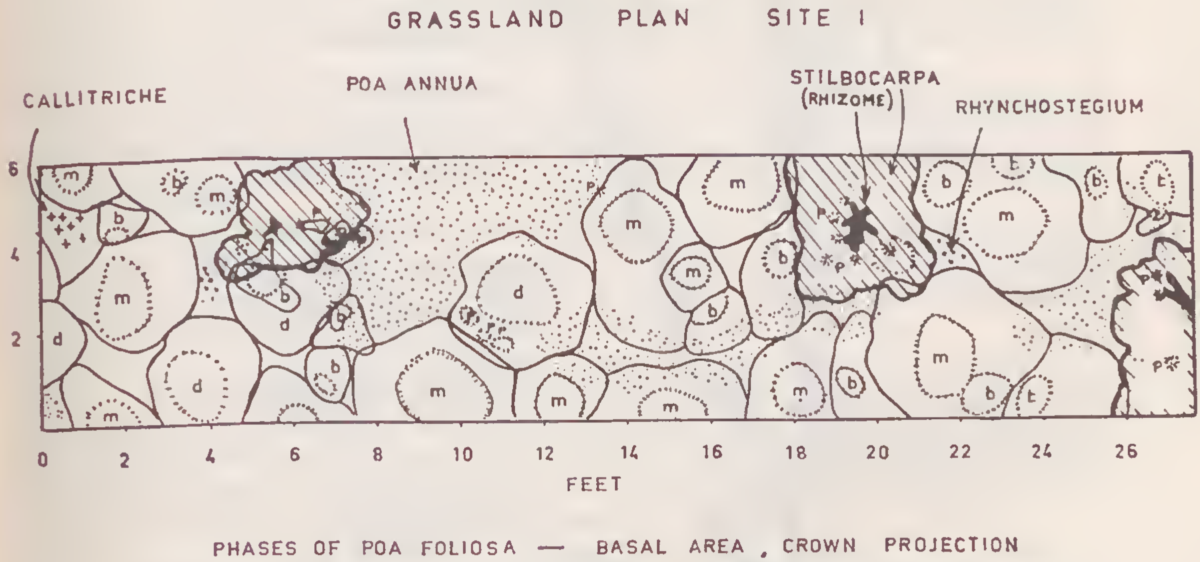


Fig. 3—Plan of grassland tussocks and *Stilbocarpa* patches, showing satellite crowns of *Poa foliosa* around older tussocks and the invasion of *Stilbocarpa* by pioneer *Poa foliosa*.

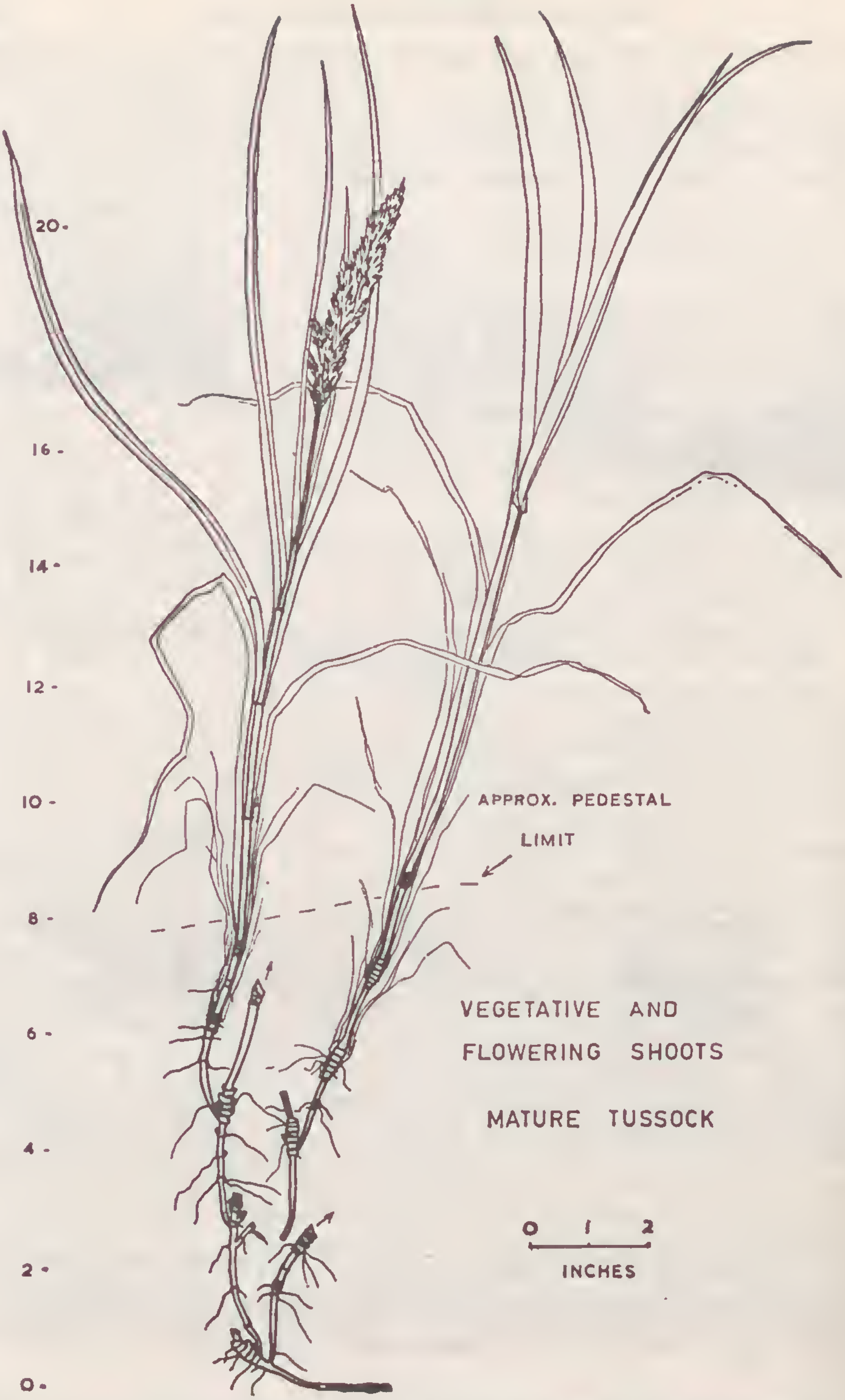


FIG. 4—Excised vertical rhizomes of *Poa foliosa* from large mature tussock site 2, showing sympodial growth associated with flowering shoot and monopodial growth of the vegetative shoot. Each short shoot is separated by one long internode.

Where monopodial growth occurs, successive short shoots are separated by single long internodes. It is possible that a long internode is produced at the commencement of growth in spring, and that one short shoot is produced each year (Fig. 4). The apical bud is buried by dead sheath litter and roots to a depth of ½-2 in. Roots are profusely developed, chiefly from the lower nodes of the short shoots.

In the flowering condition, four green leaves occur below the inflorescence and the internodes are greatly elongated. The die-back which takes place after flowering may extend to include the whole short shoot. Dead shoots with no evidence of flowering culms also occur within the pedestal. These are presumably vegetative, although it is possible that a flowering condition may have been induced in them but not expressed (Dr M. B. Gott pers. comm.). In some cases a short shoot may remain alive as a dormant unit after having been separated by decay from the parent rhizome. The stimulation, dormancy, and death of the axillary buds are important features which affect the habit and longevity of the grass. The small proportion of axillary buds which ultimately develop in *Poa foliosa* do so when the subtending leaf or bract is dead. Branches thus tend to occur in the lower half of the short shoot, or in the older parts of the long shoots. After the cessation of growth of the long shoot, a complex cluster of short shoots may develop. A similar paucity of bud expression has been described for *Poa pratensis* by Etter (1951) who related tiller production to environmental factors and the morphology of the sward. Aspinall (1964) and Langer (1963) also point out the complexity of factors controlling tiller production. The centre of *Poa foliosa* tussocks appears to be less favourable for vegetative growth and flowering than the periphery. This effect was noted in *Bromus inermis* by Lamp (1952), who ascribed this difference to greater mutual shading; however, it could also be due to greater competition for nutrients or the presence of inhibitory substances.

In the young tussock, long shoots are relatively common and often grow downwards and outwards to a depth of 6-8 in. and emerge near the base of the pedestal (Fig. 5). There is a tendency for short shoots to be concentrated in the upper 2-4 in. Dead rhizomes are not common. In general the crown is fairly open and the litter sparse.

In older, but still upright tussocks, the long shoots are orientated vertically and have horizontal branches which tend to descent towards the periphery of the pedestal. Remains of short shoots are found at the base of the pedestal, but living shoots occur only in the uppermost 4-5 in. Litter is 3-5 in. thick and dead rhizomes are common.

In large leaning tussocks, old dead rhizomes indicate the original orientation of the pedestal, and the younger vertical rhizomes show the response to the new orientation. Living rhizomes extend downwards for 4-8 in., the greater depth being on the warmer and better illuminated upper side (Fig. 6).

Cyclic Development

At first sight, the grassland presents an apparently uniform pattern of tussocks but, on closer inspection, considerable variation in size, vigour, and spacing can be found. The unit of pattern, based on crown vigour, can be classified into four broad categories which are similar to the phases recognized by Watt (1947) for the regeneration of community dominants.

Phases

Pioneer Phase: The plants are small and scattered and bear few tillers; the rhizomes which bear the short shoots may be widely branched, and may or may

FIG. 5—Longitudinal section of a Building phase tussock showing rhizome development in the pedestal. Dead rhizomes are fully black.

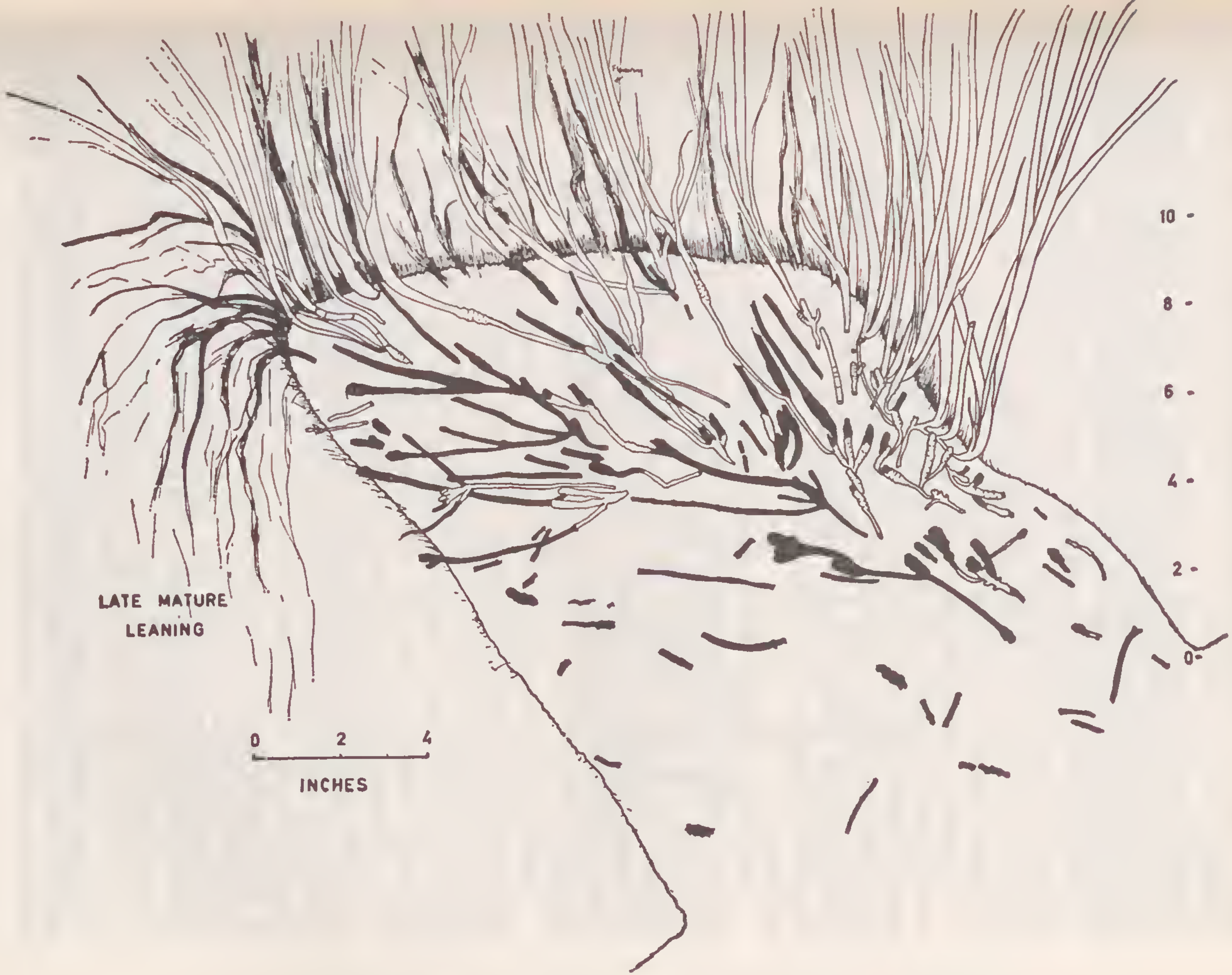


FIG. 6—Longitudinal section of old mature tussock that had been leaning downhill. This shows the prior orientation of early rhizomes now dead and the copious present development of short shoots on the uphill side of the pedestal.

not be attached to the parent tussock or invasion front. This phase also includes seedlings.

BUILDING PHASE: The plants are taller and tend to form small or embryonic tussocks. In an invasion front this phase is spread out as a definite band. The amount of dead leaf litter is small and the pedestal is absent or rudimentary. This phase may occur as small marginal offshoots from Mature or Degenerate tussocks.

MATURE PHASE: The plant reaches its maximum height for the site and the pedestal is tall and well developed. On slopes the whole tussock may lean down hill. The amount of dead leaf material in the crown is greater than in the Building phase, but is less than that of the green leaves. This phase may also be present as a marginal crown of a degenerate tussock.

DEGENERATE PHASE: The plant shows reduced vigour with shorter leaves than in the mature phase and with a greater proportion of dead to living leaves. The pedestal remains large and conspicuous. In many cases, especially on gentle slopes, the Degenerate phase may be to some extent masked by the development of Building phase satellites which have merged with the periphery. If these do not develop, however, the whole tussock will ultimately die. In other cases a half-grown tussock may degenerate, thus omitting the Mature stage. The causes of death are unknown.

GAP PHASE: This represents the space between the *Poa* crowns and may contain prostrate pedestals of living tussocks or the humifying stumps of earlier pedestals. These sites may eventually become hollows as they decay and the tussocks rise around them. In this respect, the growth of the peat is analagous to that of the regeneration complex of a blanket bog (Godwin & Conway 1939). The Gap phase is considered in terms of the dominant plant, i.e. *Poa foliosa*, and, therefore, may consist of bare peat or contain colonies of liverworts and mosses, *Poa annua* sward, small herbs such as *Epilobium nerteroides*, *Cardamine corymbosa*, and *Callitriche antarctica*.

The age of various phases is not known with certainty, but some deductions can be made from the ANARE station activities on Camp Hill and Wireless Hill (Site 2) since 1948. A plastic water pipe, which was laid across the slope at Site 2, had been overgrown by Late Building phase tussocks of *Poa foliosa* by 1963, indicating that this phase develops on this site in less than 5-6 years. Similarly, radio-aerial wires blown down in 1952 were overgrown by mature tussocks by 1963. This means that 6 in. of pedestal peat can develop in less than 11 years.

If one short shoot is produced each year on a vertical monopodial rhizome, then the top 7 in. of peat in a late mature pedestal can develop in 9 years. It is possible that the Mature and Degenerate phases persist for a very long time, since the great majority of tussocks are in this condition. C^{14} analyses* of the basal peat of mature pedestals 18-22 in. high, indicate an average age of 50 ($+50-30$) years B.P. (1950).

[* Analyses were carried out by T. A. Rafter, Institute of Nuclear Sciences, D.S.I.R., New Zealand, specimens R1421/2, R1421/3, N.Z. sheet grid reference numbers.]

PATTERN AND PROCESS IN THE *Poa foliosa-Cardamine corymbosa* ASSOCIATION

In this association at Sites 2 and 3, the pattern of the tussocks shows a fairly close and even spacing of Mature and Degenerate tussocks with smaller vigorous tussocks of the Building stage and gaps and hollows of various sizes (Pl. 27, fig. 3).

In small gaps the whole space may be filled with litter and only sparse bryophytes of extreme shade tolerance are present. In larger gaps patches of *Callitriche antarctica, Cardamine corymbosa, Acaena adscendens, Agrostis magellanica,* and bryophytes such as *Metzgeria furcata, Pterygophyllum dentatum,* and *Amblystegium serpens* occur. On the southerly slope at Site 2, the luxuriance of the tussocks decreased the light penetrating to the floor of the gaps, and the associated species were very sparse. Gaps of 3 ft, 1-1¼ ft, and ½ ft in diameter had light intensities on the floor of 57%, 26%, and 3·8% respectively.

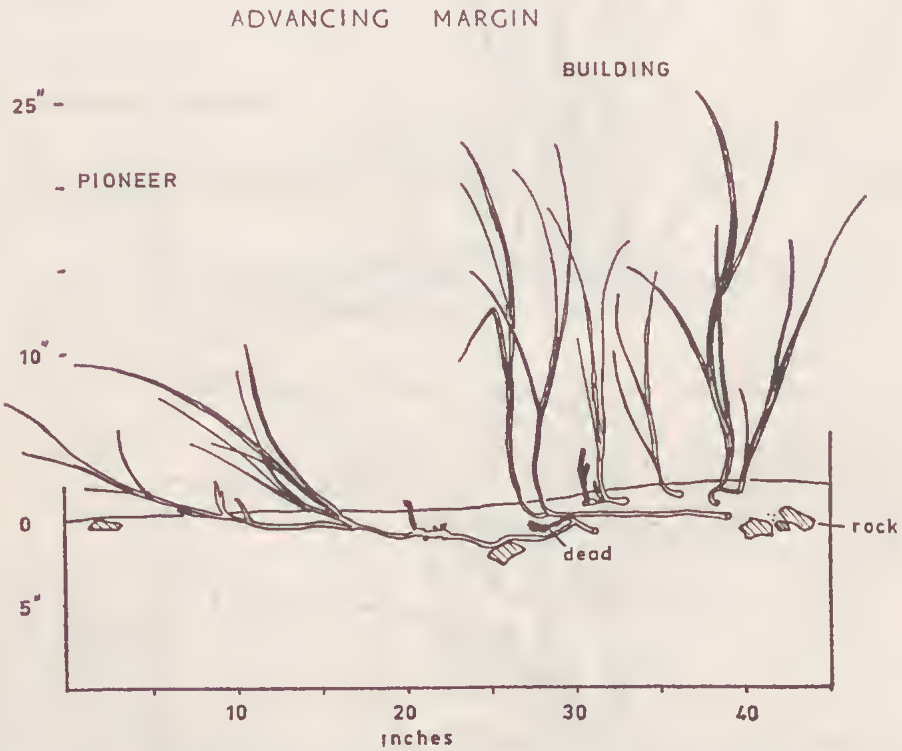


FIG. 7—Profile of the advancing margin of *Poa foliosa* into the short turf of *Festuca erecta* and *Agrostis magellanica*. Only *Poa foliosa* is shown.

Regeneration of *Poa foliosa* takes place almost exclusively by long shoots developing down the upper side of prostrate peat pedestal at depths of 1-2 in. The steep 'cliff' of such pedestals is overhung with a dense accumulation of litter. Although some shoots do curve downward and break through the thatch-like litter, most do not take root. This accumulation is thus likely to remain a major barrier to the forward advance of the rhizomes. The Pioneer shoots may develop into the Building phase adjacent to the old crown, or may extend and branch at wide angles throughout the gap. In one gap studied, five such widely spaced pioneer plants were linked by rhizomes to a Late-Building tussock. In another, the presence of three dead tillered-rhizome clusters indicated that the establishment of these young plants is not always assured. Three definite seedlings were found on Site 2; one occurred on the floor of a large gap 3 ft in diameter (Fig. 10), and the other two were found on old exposed pedestal mounds.

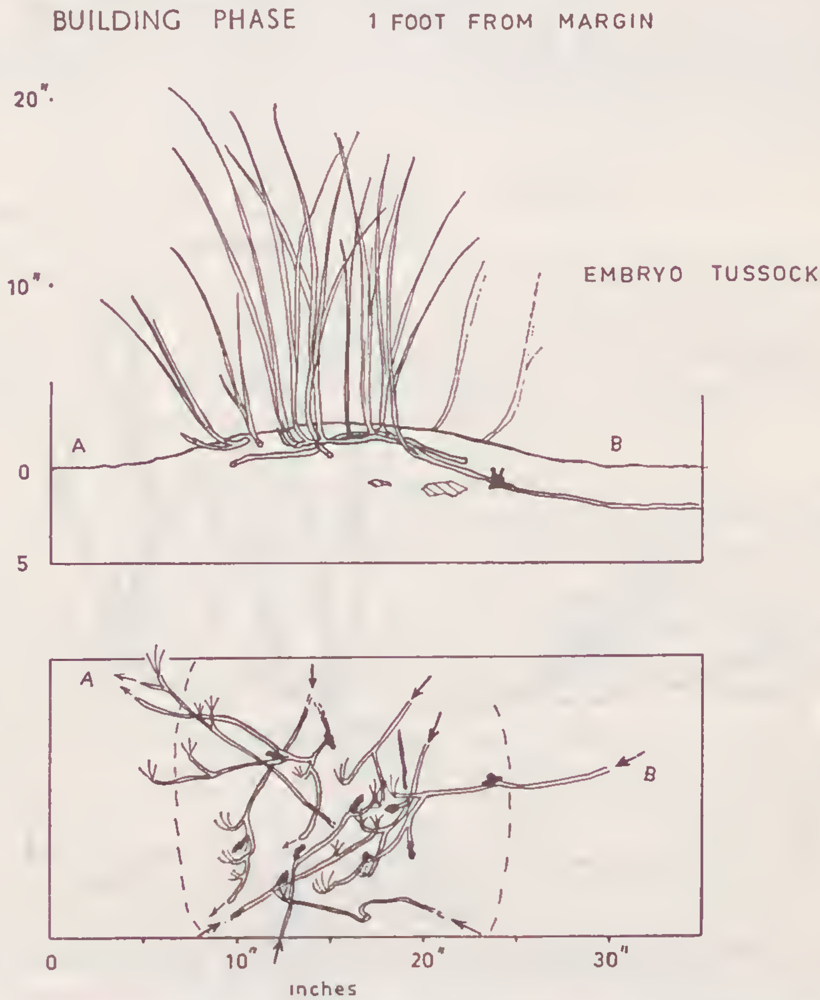


Fig. 8—The development of an embryonic tussock by convergence of various rhizomes. Dead areas are black, arrows indicate the direction of travel of the rhizome, and the terminal leafy short shoot is conventionalized.

Around the periphery of stabilized landslips in both sites on Wireless Hill, the developmental phases are displayed in parallel bands instead of being confined to the normal mosaic pattern (Pl. 27, fig. 2). In Site 3, the pioneer zone extends 4-6 ft from the margin proper and shoots 4-6 in. high emerge at low angles from rhizomes 1-3 in. deep (Fig. 7). Near the margin the advancing shoots are often orientated at right angles to the front. Well away from the margin the branching of the long shoots is sparse with few tillers, and death of long and short shoots is

TABLE 1

Data of the various phases of Poa foliosa

Phase	No. of tussocks examined	% of crowns	% of area	Av. height total tussock (in.)	Av. height crown (in.)	Av. height pedestal (in.)
Pioneer	10	4	0·1	12	12	0
Early Building	7	12	2·3	23	23	0
Late Building	17	12	11·2	31	25	6
Mature	38	56	58·2	39	26	13
Early Degenerate	11	8	5·2	37	26	11
Late Degenerate	6	8	6·4	30	17	12
Gap	—	—	16·6	—	—	6*

* Very variable (0-10″)

Cover estimates and a qualitative species list are given in Tables 2 and 3 (increasing number of point quadrats from 50-75 lowered the % cover of estimates of *Poa foliosa* by only 1-2%).

TABLE 2

% Cover and Cover Repetition, Site 3, Wireless Hill, 16 December 1963, using 75 Point Quadrats for each Determination*

Species	Invasion Front				Hinterland		
	Pioneer		Building		Tussock		
	% Cover	Cover Reptn	% Cover	Cover Reptn	% Cover	Cover Reptn	% Cover
	using descending point						using ⅛″ dia. pin
Poa foliosa	13	1·00	64	1·54	71	2·22	76
Festuca erecta	29	2·46	7	1·60	—	—	—
Agrostis magellanica	33	1·40	4	1·00	1	1·00	—
Luzula campestris var. *crinata*	27	1·50	1	1·00	—	—	—
Montia fontana	23	1·18	1	1·00	—	—	—
Acaena anserifolia	12	1·22	9	1·00	—	—	3
Ranunculus biternatus	9	1·00	—	—	1	1·00	—
Stilbocarpa polaris	4	1·33	—	—	—	—	1
Pleurophyllum hookeri	3	1·00	—	—	—	—	—
Epilobium linnaeoides	1	1·00	—	—	—	—	—
Colobanthus crassifolius	1	1·00	—	—	—	—	—
Cardamine corymbosa	—	—	1	1·00	—	—	3
Stellaria decipiens	—	—	—	—	—	—	1
Callitriche antarctica	—	—	—	—	—	—	1
Bryophytes	24		4		3		3
Tussock of *Poa* only	—		—		3		3
Litter	65		96		86		88
Bare Peat	3		—		8		8
Total living vegetation	93		73		73		80
Total soil cover	99		100		92		91

* Number of hits per pin.

common. The Building zone is clearly defined as a rank, uniform lawn 9-15 in. high and 4-12 ft wide. Here, considerable proliferation of short shoots has occurred. Detailed excavations made in 1962 reveal that some aggregation of shoots has taken place, even though the rhizomes are unconnected and apparently growing in random directions (Fig. 8). A similar morphological basis of clumping pattern has been described for *Calamagrostis neglecta* by Kershaw (1963) and for *Poa australis* var. *latifolia* by the author (unpublished). Therefore, at these points of rhizome convergence a young crown of *Poa foliosa* could accumulate an embryonic pedestal of peat due to the greater local concentrations of litter, fine roots, and rhizomes. It is possible, therefore, for such crowns to consist of more than one genotype. The Mature zone is marked by tall dense tussocks and extends for a further 4-12 ft. Here, the tussock habit is accentuated because the rhizomes are limited to the top 4-5 in. of the peat and are confined to the pedestal when this height is exceeded.

During the Building and Mature phases the competition exerted by *Poa foliosa* is at a maximum and many species are suppressed. Beyond this zone the tussock grassland displays greater diversity in structure due to degeneration, death, and regeneration. This is the hinterland region described by Watt (1943, 1947). Many of the species of the seral community reappear sporadically in this region and, in the relative isolation of each gap, they may achieve local abundance.

Features of the phases of *Poa foliosa* compiled from transects and quadrats on all sites are set out in Table 1. The details of floristics and % cover of the

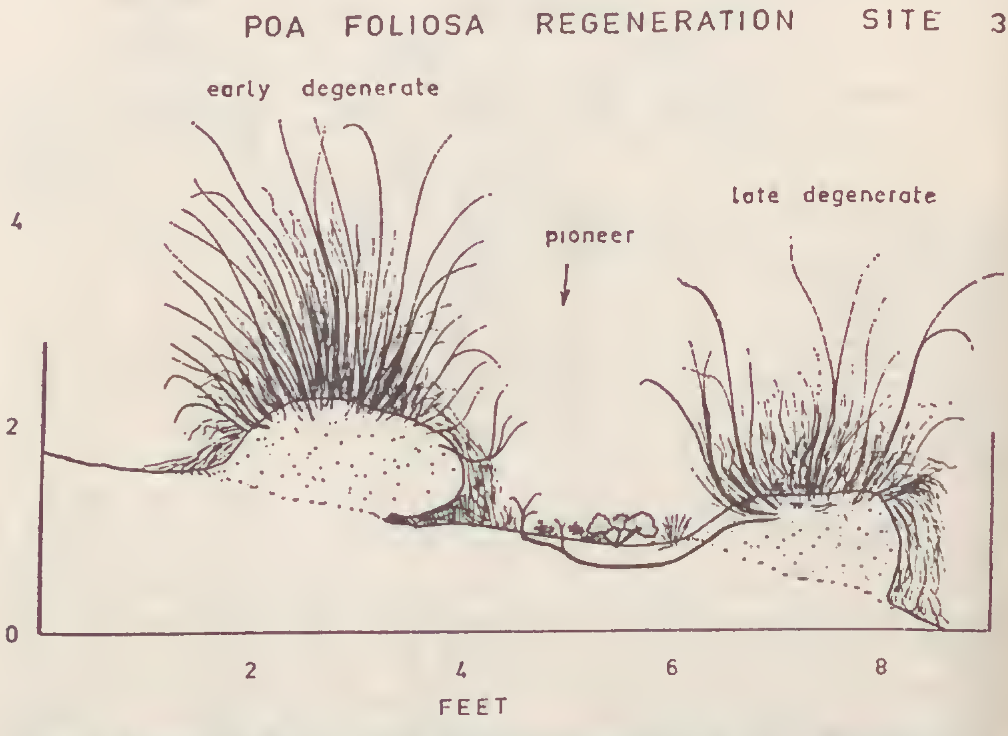


FIG. 9—Regeneration of *Poa foliosa* in the hinterland region at site 3, by means of a long shoot at shallow depths. Pedestals on this site may not be as deep as in other areas and rhizomes can spread out into gaps. A seedling *Stilbocarpa* is also shown.

TABLE 3

Species Present in 3 Phases—Site 3, Wireless Hill, December 1963

Species (Cryptogams in brackets)	Invasion Zone		Hinterland Tussock
	Pioneer	Building	
Epilobium linnaeoides	+		
E. nerteroides	+		
(*Rhacomitrium crispulum*)	+		
(*Thuidium furfurosum*)	+		
(*Lophocolea tenax*)	+		
Acaena anserifolia var. *minor*	+		
Colobanthus muscoides	+		
Festuca erecta	+	+	
(*Bartramia papillata*)	+	+	
(*Amblystegium serpens*)	+	+	
Colobanthus crassifolius	+		+
(*Peltigera polydactyla*)	+		+
(*Ditrichum strictum*)	+		+
(*Hypnum cupressiforme*)	+		+
Poa foliosa	+	+	+
Agrostis magellanica	+	+	+
Montia fontana	+	+	+
Ranunculus biternatus	+	+	+
Luzula camprestris var. *crinata*	+	+	+
Acaena adscendens	+	+	+
Stilbocarpa polaris	+	+	+
Pleurophyllum hookeri	+	+	+
Stellaria decipiens	+	+	+
Cardamine corymbosa	+	+	+
(*Metzgeria furcata*)	+	+	+
(*Lophocolea lenta*)	+	+	+
Callitriche antarctica			+
(*Pterygophyllum dentatum*)			+
Total	26	15	18
Vascular plants	16	11	13

phases of *Poa foliosa* in the invasion of the landslip community of *Agrostic-Festuca-Pleurophyllum* on Site 3 are given in Tables 2 and 3.

PATTERN AND PROCESS IN THE *Poa foliosa-Stilbocarpa polaris* ASSOCIATION

In Site 1 the canopy of *Poa foliosa* is abruptly interrupted by clusters of large hairy crenate leaves of *Stilbocarpa polaris*. In this N.-facing and presumably warmer site, the peat accumulation is less than 6-12 in. above the old scree, and peat pedestals were smaller and not leaning as on the other sites. In some cases, daughter crowns may develop 2-3 in. from the periphery of Mature or Degenerate tussocks by the emergence of tillers through the litter layer.

The phases of development of *Stilbocarpa* are clear from the Pioneer seedling to the Mature plant. Most *Stilbocarpa* appears to be in the late Building to Mature phase with large leaves 20-24 in. long arising from rhizomes 3-9 in. long and 1-2 in. broad. Growth is monopodial and inflorescences and side branches occur close to the apex of the rhizome. Only when the thickened axillary rhizomes are cast off by the progressive death of the parent rhizome are they regarded as constituting an appropriate phase. Some shoots appear to be liberated at a stage equivalent to the Building phase. Occasionally, the whole plant dies and leaves a

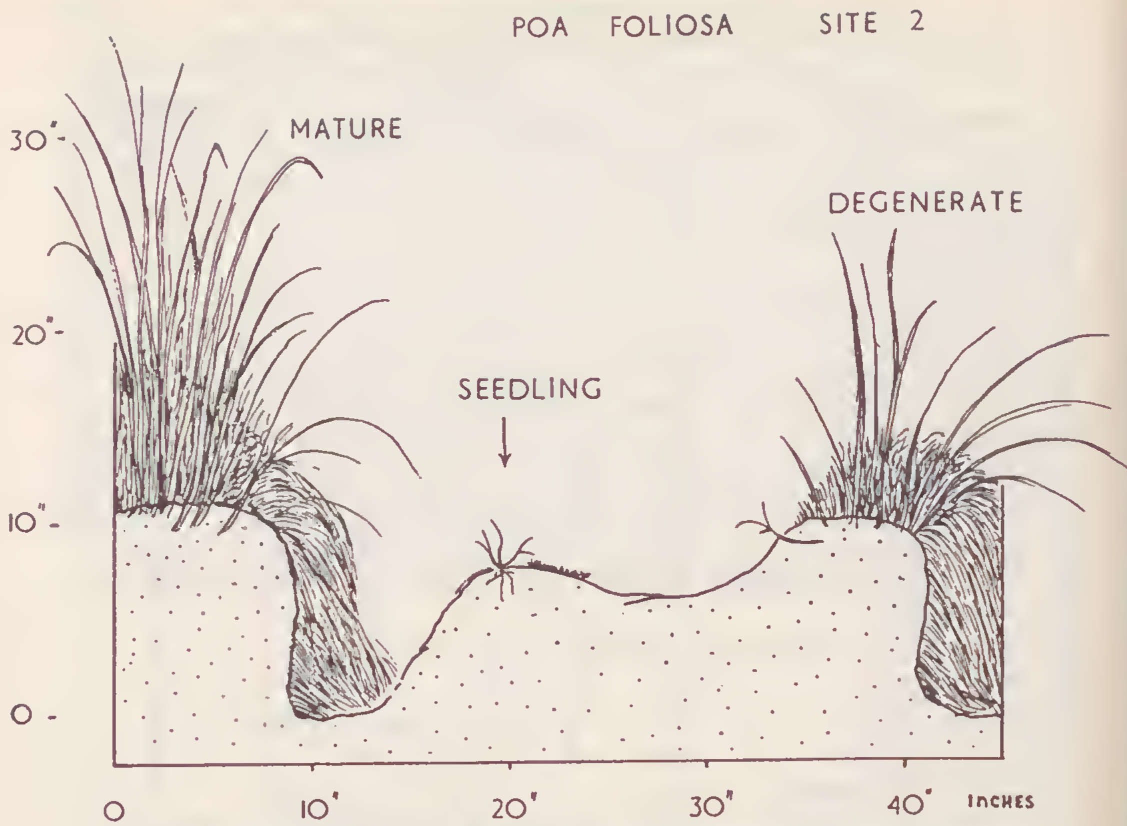


FIG. 10—Regeneration of *Poa foliosa* in site 2 where rare seedlings may be found on old pedestal mounds in gaps associated with *Callitriche antarctica*. Heavy infestations of the grain fungus *Claviceps* sp. may reduce seed supply in this area.

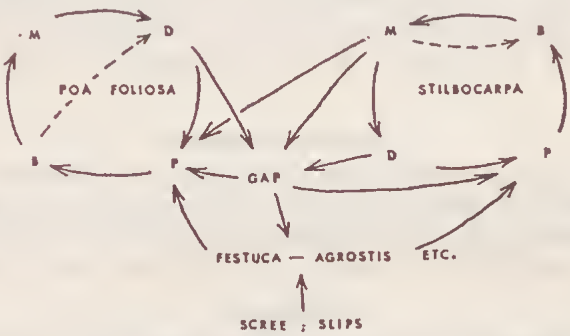
gap in which the vascular fabric of the rhizome is the only evidence of previous occupation. Degenerating plants, however, were rare, possibly due to the rapid decay of their fleshy leaves and rhizomes.

In large patches of *Stilbocarpa*, the pattern of development and regeneration is less obvious than that in the grassland areas. Gaps are created only where the haphazard rhizomes diverge; where Mature plants follow each other closely no gaps are formed. Gaps may be recolonized by rhizomes or seedlings of *Stilbocarpa*. In areas of mixed tussock and *Stilbocarpa*, gaps may sometimes contain exceptionally dense swards of the introduced *Poa annua*, or prostrate mats of *Callitriche antarctica* and the moss *Amblystegium serpens*. Seedlings of *Stilbocarpa* occur occasionally (Fig. 9). In some small patches between the *Poa foliosa* tussocks, the rhizomes of *Stilbocarpa* may grow centrifugally, or may be oriented so that the retreating rhizome leaves a bare area which is passively invaded by pioneer rhizomes of *Poa foliosa* from the adjacent tussocks. Active invasion can also take place by rhizomatous Pioneer *Poa foliosa* growing up through the canopy of *Stilbocarpa*. It seems likely, therefore, that *Poa foliosa* will ultimately assert its supremacy in this association, leaving *Stilbocarpa* to fit into the general pattern which is imposed on it. The very large patches of *Stilbocarpa* on newly stabilized slopes are likely to be sub-climax to *Poa foliosa* in the peat-slip succession. The position of the equilibrium attained after the invasion and establishment of *Poa foliosa* will depend, no doubt, on the exact nature of the site factors. *Poa annua* is likely to remain a gap species as it is readily suppressed by dense litter of *Poa foliosa.*

General Considerations

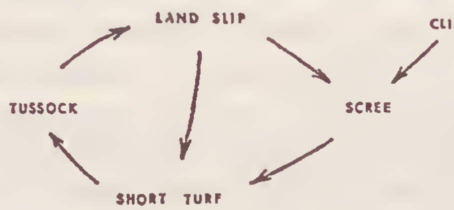
The phases of *Poa foliosa* show different reactions to sheep grazing on Wireless Hill. Here, the Mature and Degenerate tussocks have been killed, leaving large areas of bare pedestal mounds. The Building and Pioneer stages, with their shoots growing close to the ground, have been little damaged. The repeated removal of photosynthetic tissue and nutrients could lead to a serious decline in the vulnerable Mature and Degenerate phases, especially if the mass of roots and rhizomes confined to the pedestal are dependent on the nutrient cycle of litter decay.

A generalized scheme for cyclic development in ungrazed maritime tussock grassland is as follows:



P, B, M, D = phases of development; for arrows read 'becomes'.

The broad-scale pattern development of the grassland is also cyclic over a very long time-scale, e.g.



Comparisons of photographs from Wireless Hill by Hamilton in 1914 (1926) and Jenkin in 1965 (Pl. 27, fig. 1) show relatively minor changes. In some cases landslips are now covered with short turf, but in the windiest sites they are still bare. The stabilized scree slope in Site 1 was only lightly vegetated in 1914, and very large tussocks now occupy the upper portion of the wind scoured sand slope at the SE. part of the isthmus.

The rate of turnover of each cycle is not known, but the life of the individual dominant plants is probably of the order of several decades. Growth rate of the vegetation is unexpectedly high for grasslands. December estimates of the dry weight of the *Poa foliosa-Cardamine corymbosa* association at Site 2 are 0·96

Kg/M² for tops and 1·94 Kg/M² for roots to 6 in. The regrowth of the stand one year after close clipping varied from 1/10 to 1/2 of the original dry weight. The high root weight is probably the reason for the rapid build-up of the pedestal under conditions not favouring decomposition. *Poa foliosa* grassland develops a leaf area index of about 4 in December, but the interception of the predominantly diffuse light varies according to the phase of growth. The abundance of standing litter in the late Mature and early Degenerate phase may deprive the young shoots of a significant amount of light. *Stilbocarpa* shows a marked initial decrease in light intensity with depth, due to the horizontal foliage, but the light is very variable and the pools of bright diffuse light could be sufficient to permit pioneer *Poa Foliosa* to succeed.

It would be of considerable interest to know why *Poa foliosa* is able to grow so luxuriantly in such a uniformly cool and cloudy environment. The growth of transplants in the warmer climate of Melbourne is very poor, in spite of careful watering. If this species reaches optimum growth rates at relatively low temperatures, then the growing season at Macquarie Is. could be long. Experiments under controlled conditions are being initiated to test this hypothesis. Details of the seasonal biomass and leaf area index changes in the grasslands and herbfields are being determined by J. F. Jenkin, ANARE, Macquarie Is., and will be published in due course.

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Explanation of Plate

Plate 27

Fig. 1—General view of Macquarie Is. S. from Wireless Hill. Photograph by J. F. Jenkin 1965, from the same place as that taken by Hamilton in 1914. ANARE station on the isthmus.

Fig. 2—The re-establishment of *Poa foliosa* grassland in a landslip succession on Wireless Hill. A front of *Poa foliosa* is advancing as a rank lawn into a short turf of *Agrostis, Festuca*, and *Luzula*. The mature grassland in the hinterland area has developed the typical tussock form and pattern. The large rosettes in the seral turf are of the composite *Pleurophyllum hookeri*.

Fig. 3—Close view of the *Poa foliosa* sward showing the magnitude of the tussocks; the trapper spade is 3 ft high. The pattern consists of building, mature, degenerate, and gap phases.